

WHY DO GRASS OWLS (*TYTO CAPENSIS*) PRODUCE CLICKING CALLS?

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ABSTRACT.—Flying Grass Owls (*Tyto capensis*) continuously produce double clicks and trains of single clicks with an emphasized frequency of 1.9 kHz. Double clicks have a click rate of seven per second while click trains have a rate of 32 single clicks per second. We examined the possible role that clicking could play in echolocation or in prey capture. The owls did not increase clicking when no moonlight was available. In most cases the birds landed at the roost without clicking. Spectral analysis using a dead Grass Owl showed that the facial mask was directionally insensitive to sounds at 2 kHz. An echolocative function was thus unlikely. Neither of the prey rodents (*Otomys angoniensis* and *Mastomys natalensis*) reacted to recorded Grass Owl clicks. The clicks, therefore, probably did not play a role in prey capture. We present evidence that clicks are involved in social communication between Grass Owls.

KEY WORDS: *Grass Owl*; *Tyto capensis*; *echolocation*; *prey location*; *communication*; *territoriality*.

Porque *Tyto capensis* emite vocalizaciones “click?”

RESÚMEN.—*Tyto capensis* continuamente produce “clicks” dobles y seriados de un solo “click” con una frecuencia de 1.9 kHz. Los “clicks” dobles tienen una tasa de siete por segundo mientras que los seriados tienen una tasa de 32 “clicks” individuales por segundo. Examinamos el posible papel de las vocalizaciones “click” con la ecolocalización o en la captura de presas. Las lechuzas no aumentaron estas vocalizaciones sin luz de luna. En la mayoría de los casos las aves llegaron a las perchas sin producir sonido. El análisis del espectro utilizando un *Tyto capensis* muerto demostró que el disco facial fué direccionalmente insensible a sonidos de 2 kHz. Por lo tanto la función de ecolocalización fué descartada. Tampoco los roedores presa (*Otomys angoniensis* y *Mastomys natalensis*) reaccionaron a las grabaciones de vocalizaciones “click” de *Tyto capensis*. Por lo tanto las vocalizaciones “click” probablemente no juegan un papel en la captura de presas. Presentamos evidencias que las vocalizaciones “click” están involucradas en la comunicación social de las lechuzas.

[Traducción de César Márquez]

The Grass Owl (*Tyto capensis*) is a Red Data Book Species which inhabits grasslands, usually in long grass and often in the vicinity of water (Steyn 1982). Although it is mainly nocturnal, it occasionally hunts during daylight (Steyn 1982). Tytonid owls produce loud bill snapping or clicking sounds under conditions of fear or aggression (Campbell and Lack 1985). Walker (1974) and Bunn et al. (1982) found breeding Barn Owls (*Tyto alba*) using a peculiar rapid vocal clicking call and suggested that this may be connected with courtship, excitement, or intimidation. Little is known of Grass Owl vocalizations but they emit sharp clicking calls during flight, presumably by repeatedly flicking the tongue against the palate (Steyn 1982, Kemp and

Calburn 1987, Erasmus 1992). Grass Owls are exceptional among the owls in that these calls, which have never been described quantitatively, are emitted almost continuously in flight. This requires explanation. There are three hypotheses explaining these clicking sounds. The first is that the clicks are used for echolocation. Since the owls cannot see in absolute darkness and have to rely on a detailed knowledge of local topography during dark nights (Campbell and Lack 1985, Martin 1986), clicking sounds enable them to echolocate obstacles (Kemp and Calburn 1987). Curtis (1952) (cited in Payne 1971) found the performance of Barn Owls in avoiding obstacles to be dependent on available light and concluded that Barn Owls do

not echolocate. Both Oilbirds (*Steatornis caripensis*) and Cave Swiftlets (*Aerodromus* spp.) perform echolocation by means of clicking sounds (Schnitzler and Henson 1980) associated with obstacle avoidance (Medway 1967, Fenton 1975, Schnitzler and Henson 1980). There are two types of echolocative sounds: broadband clicks and more complex calls (broadband or narrowband, Fenton 1980). Broadband clicks are used by Oilbirds comprising a rapid burst of sound impulses lasting up to 25 ms. Some swiftlets and megachiropteran fruit bats emit double clicks with an internal interval of 15–40 ms. The mask and external ear of tytonid owls have several adaptations which increase auditory acuity (Bunn et al. 1982) and which could potentially aid in echolocation. Payne (1971) investigated the acoustic abilities of Barn Owls, and concluded that asymmetrically-placed ear flaps, feathers that are modified to reflect sound and held in a tightly packed and almost parabolic wall, and even the characteristic position in which the head itself is held (downward tilting) are all adaptations involved in hearing. Grass Owls share these characteristics. Payne (1971) conducted playback experiments to dead Barn Owls and found a positive relationship between directional sensitivity and increasing frequency. However, these experiments only took into account the external structure of the facial mask and not the neural basis of hearing which may, in itself, strongly affect owl hearing and which may assist echolocation.

The second hypothesis for clicking calls is that they are used for prey stimulation. The clicking calls of Grass Owls could be a means of stimulating rodents into activity, causing them to reveal their whereabouts (Kemp and Calburn 1987). Given the well-developed auditory power of owls (Campbell and Lack 1985), this would facilitate the capture of prey. The majority of studies on the influence of owl activity on rodents concern owl foraging behavior and rodent use of microhabitat (Abramsky et al. 1996, Thompson 1982, Brown et al. 1988, Longland and Price 1991). However, none of these studies measured the initial reaction of rodents to owl-generated cues but rather at the longer-term activity patterns of the rodents in response to predation.

A third hypothesis suggests that clicking calls are used for intraspecific communication. Erasmus (1992) noted that Grass Owls often click when in the vicinity of their breeding site. This gives rise to

the hypothesis that the clicks are used as signals between Grass Owls.

The aims of this study were, firstly, to give a quantitative description of the clicking call of Grass Owls and, secondly, to test the three hypotheses.

METHODS

During March and April 1997, recordings were made on 22 occasions (1800–2300 H) at Rietvlei Dam Nature Reserve, Pretoria (25°54'S, 28°18'E) using a Sony TC-D5M cassette recorder with a Sony ECM-1035 directional microphone. The frequency response of the recording system was 30 Hz–18 kHz within 4 dB. Most of the recordings were made at two Grass Owl roosts. The first was located in a temporary marshland and inhabited by a Grass Owl pair. The second roost, from which only a single Grass Owl was flushed, was located in a permanent marsh at least 1 km from the first roost. During recording sessions the observer sat approximately 15 m from the roost. Visual observations of the owls were made when possible. Three different light classes were identified using the phase of the moon: (1) full moon, waxing and waning gibbous, (2) waxing and waning crescent, first and last quarter, and (3) no moon. The number of click sequences heard per observation hour was calculated for each of the three light classes.

We characterized the spectral and temporal properties of each recording using Canary 1.2 (Cornell Laboratory of Ornithology) on a Power Macintosh 7100/66 computer. Except for some click trains which were too short in duration, we performed 30 measurements of each of the six parameters (Fig. 1 and Table 1) for a particular recording. The means of these values were used for describing the clicks and for comparing clicks emanating from owls at the two main roosts. Recorded calls were usually in the form of click pairs or as trains of single clicks. Since the amplitude of the recorded clicking calls varied depending on the distance between the microphone and the owl, detail of spectral range also varied. For this reason the emphasized (peak) frequency was the only spectral characteristic measured (Table 1).

To measure the directional hearing characteristics of Grass Owls, we played sounds to a dead Grass Owl; an undamaged road casualty. Due to the protected nature and rarity of this species, other carcasses could not be obtained. Measurements were conducted in an anechoic chamber provided by the South African Bureau of Standards (SABS). We connected a Bruel and Kjaer (B & K) 1405 noise generator to a B & K 1617 filter; the latter was, in turn, connected to a B & K 2706 amplifier which drove a Philips AD11400 tweeter loudspeaker (LS) through which pink noise of $\frac{1}{3}$ octave was played to the carcass (2.0, 10.0, and 12.5 kHz, respectively). We mounted the LS on a flat metal baffle on a tripod. We used a B & K 4165 calibration microphone, calibrated by means of a B & K 4230 calibrator, to measure the frequency response of the LS. We then determined the frequency response of a G-196 miniature electret microphone (Matsushita Corporation). The weakest response was at 12.5 kHz where the signal-to-noise ratio was better than 11 dB. This microphone and an OP07 buffer amplifier were imbedded in resin and placed in the dead owl's head from

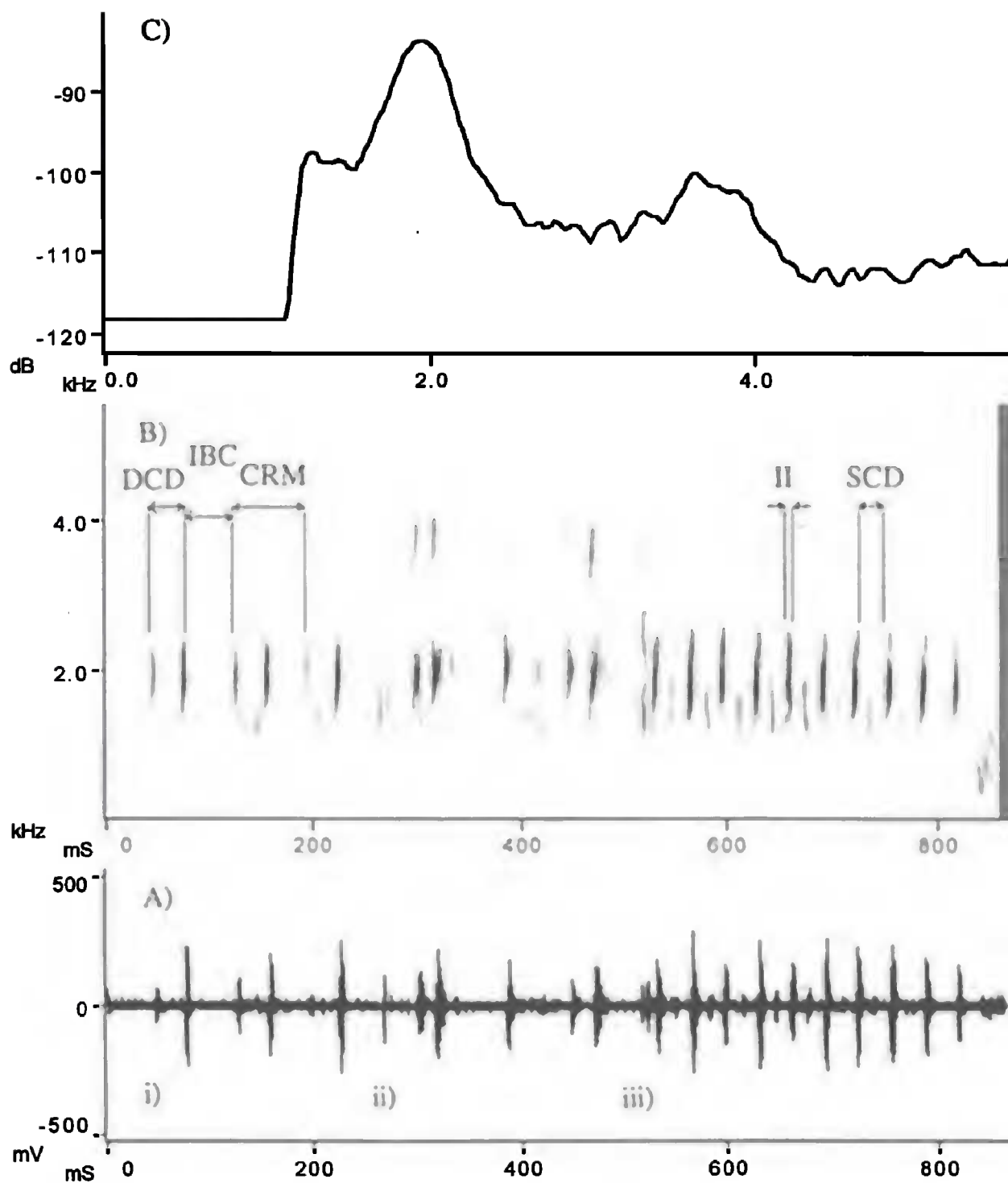


Figure 1. Graphical representations of Grass Owl clicking calls. (A) Oscillogram depicting (i) double clicks recorded at roost 1, (ii) double clicks recorded at roost 2 and (iii) a click train recorded at roost 2 indicating call durations and the temporal characteristics of sound amplitude. (B) Spectrogram of the same sounds. (C) Frequency spectrum of clicks in parts (i) and (ii), above, indicating a single emphasized frequency just below 2 kHz with no significant energy between 2 kHz and 10 kHz. Energy below 1 kHz, resulting from background noise, has been filtered out. Analysis of Fig. 1a, b: FFT size 1024 points; frequency grid size 21.53 Hz. Analysis for Fig. 1c: FFT size = 2048 points, frequency grid size = 10 Hz. The important parameters measured for these calls are indicated on this figure. Double clicks from roost 1 and from roost 2 differ in the durations of single clicks (SCD), the presence of clear harmonics and many other characteristics (Table 1).

above so that the diaphragm of the microphone occupied the position formerly taken by the tympanum of the right ear. The owl was strapped to a mount on a tripod in such a position that the microphone was 1 m from the LS. The microphone was connected to a B & K 2610 measuring amplifier from which the output was measured in microvolts and transformed to relative sound pressure values in dB. Readings of the microphone output were taken through angular increments of 5° in the

horizontal plane of the owl head, starting from 90° with respect to the forward orientation.

Rodent trapping was performed close to the owl roost sites used for sound recordings, enabling us to decide on suitable rodent species for playback experiments. During May 1997, 100 Sherman live traps were set for 1000 trap nights in the vicinity of roost 1, where owls were regularly observed flying parallel to the marsh. Four trap lines, each with 25 traps 10 m apart, were arranged into two

Table 1. Properties of clicks recorded near roost 1 (single bird), roost 2 (a pair) and three other roosts. Rightmost column gives results of a Mann-Whitney *U*-test, comparing the values for roost 1 and roost 2. The data for other roosts are not analyzed since these comprise observations at a collection of other sites in the study area. Number of observations varies between 20–30 per roost.

PROPERTY DESCRIPTION	SYMBOL & UNITS	ROOST 1		ROOST 2		OTHER ROOSTS		<i>U</i> -TEST ROOSTS 1 & 2
		MEAN	SD	MEAN	SD	MEAN	SD	<i>P</i>
Emphasized frequency: audio frequency with the highest amplitude	EF (Hz)	1916	68	1865	95	1945	110	<0.001
Duration of double click, from start of 1st click to end of 2nd click	DCD (ms)	48	27	43	6	42	10	<0.03
Duration of an individual click	SCD (ms)	14	4	10	3	14	5	<0.001
Time duration from end of a click to the start of subsequent click	II (ms)	17	5	25	3	18	5	<0.001
Time duration from end of 2nd click of a double click to start of 1st click of subsequent double click	IBC (ms)	114	35	93	13	104	19	<0.001
Time duration from start of 1st click of a double click to start of 1st click of following double click	CRM (ms)	155	35	123	42	147	19	<0.001

grids of two trap lines per grid. Grids were 500 m apart and the lines within each grid were 50 m apart. Peanut butter with oats was used as bait and alternated with a mixture of raisins and oats in consecutive traps along a trap line. Traps were cleared twice daily at 0700 H and 1700 H. Trapped rodents were sexed, marked using toe clipping and released. Density, by species, was estimated using the Petersen density estimate (Caughley 1977) of the resulting mark-recapture data for the two grids combined. Animals were found to move between trap lines within a grid (50 m). The area covered by a grid was thus calculated as the length of the transect line 250 m and 150 m wide, thereby assuming the animals moved into the grid from at least 50 m distant. This translated to a capture area of 7.5 ha for both grids combined.

In the laboratory, rodents were subjected to recorded owl clicks. Recorded owl clicks were played to five vlei rats (*Otomys angoniensis*) and four multimammate mice (*Mastomys natalensis*) removed from the trapping site at the end of the survey. These species were used because they were the two most common nocturnal rodents with vlei rats also being a favored food item of Grass Owls (Kemp and Calburn 1987). Calls of Crowned Plover (*Stephanibyx coronatus*) and a recording of traffic in a busy street were used as control sounds, respectively, representing sounds to which the rodents were accustomed to in the field and sounds which were foreign to them. These three sounds alternated during consecutive play-

back events and each of the sounds was 25 sec in duration, separated by a silent interval of 15 sec. This sequence was recorded twice onto a four-min endless loop tape. Two glass tanks (surface 150 cm × 70 cm) were used to hold test animals. The floor of each tank was covered with white sand. In one corner was an artificial burrow, while food, water and a passive infrared detector were positioned on the other side of the tank. This area was kept clear. A rodent was placed in each tank. While one animal was tested the other was given time to settle down (>24 hr). Two time switches regulated a 12L:12D cycle, while a pair of red light bulbs remained switched on for the entire duration of the experiment. At night these provided light to record data on a Panasonic AG-455 ME video recorder. When the mouse triggered the infrared detector, a computer switched on the video camera which recorded for 90 sec. After the video camera had been recording for 10 sec, the computer activated a Panasonic RQ-L305 tape player positioned above the tank. The tape played for 40 sec (7.5 sec silence, 25 sec sound, 7.5 sec silence), after which it stopped. The video camera recorded for a further minute before it was deactivated. Each rodent's response to the three test sounds was recorded at least 10 times. Six reaction categories were identified from observation of the video recordings: (1) no movement, (2) rodent moved less than half of length of tank, (3) moved at least half of length of tank, (4) moved to opening of burrow but didn't enter, (5)

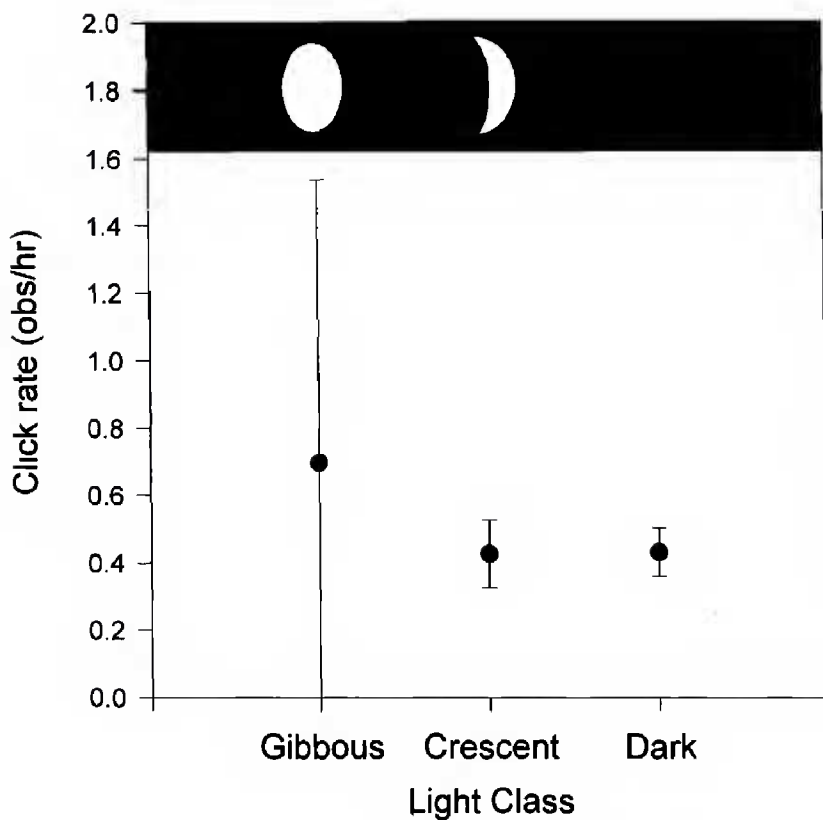


Figure 2. The frequency of Grass Owl clicking (number of owls heard per observation hour) at Rietvlei Dam as a function of the amount of moonlight. There is no trend towards an increase of clicking when no moonlight is available. Bars indicate standard deviations of observations.

ran into burrow but emerged within 10 sec or while sound still played, and (6) ran into burrow and remained there for the duration of the 10 sec or playing time. A reaction was noted for the first 10 sec of the playback (i.e., initial reaction) and also for the entire playing duration (ED) of the sound (i.e., overall reaction).

RESULTS

Field Observations. During 28 nights, we made 64 observations on Grass Owls. When landing at the roost (four observations), the owls did not click at all. On two of these occasions, the owls clicked while approaching the roost but not when landing. When taking off from the roost, the owls produced the clicking call once. While perched on the roost, they clicked on four occasions. On two occasions, owls were seen flying, then stopped clicking and landed, before almost immediately taking off again and resuming clicking. On two other occasions, two owls appearing to chase each other produced click trains. Grass Owls also answered clicks produced by other individuals. This was observed on five occasions though only one bird was visible. The owls tended to increase their clicking activity when ample light was available (Fig. 2). However, the difference in clicking activity between the three

light classes is not statistically significant (Kruskal-Wallis ANOVA, $P = 0.654$).

Spectrographic Analysis. Double clicks, comprising pairs of single clicks, were recorded during 30 observation periods. Click trains, comprising more than two single clicks following in close succession, were recorded seven times (Fig. 1, Table 1). Double clicks had an emphasized frequency of around 2 kHz (Table 1). The mean value for click trains was 1891 ± 144 Hz ($N = 7$), similar to that of double clicks. The single clicks within double clicks exhibited an internal interval (II) of some 20 ms (Table 1), compared to 20.4 ± 6.6 ms ($N = 7$) for the internal interval within click trains. The click rate measurements (CRM) for the double clicks and click trains were 123–155 ms (Table 1) and 31.6 ± 5.0 ms ($N = 7$), respectively. This corresponded to approximately seven double clicks per sec and 31.5 click train clicks per sec. The click trains, however, had a mean duration of only 275 ms ($N = 7$). Double clicks had a duration (DCD) of 42–48 ms (Table 1) and an interval between double clicks (IBC) of 93–114 ms. Single clicks within double clicks and within click trains had similar durations, respectively 10–14 ms (Table 1) and 11.9 ± 4.5 ms ($N = 7$). A Mann-Whitney U -test indicated significant differences in all the click properties produced at roost one (a single bird) compared with those emanating from roost two (a pair, Table 1).

Playback to Dead Owl. At all three playbacks to dead owls, the experimental frequencies (2.0, 10.0, and 12.5 kHz) showed a decline in amplitude of the incoming sound toward 90° (i.e., as the right ear, in which the microphone had been placed was turned away from the loudspeaker; Fig. 3). The microphone was thus shielded from the loudspeaker by the owl's head. Playbacks at 2.0 kHz indicated no clear amplitude peaks or nulls at various orientations (Fig. 3). Three such peaks were measured at 10.0 kHz. The highest was at -15° with two smaller peaks at -60° and 75° , respectively and a distinct null at -45° . Readings taken at 12.5 kHz had a distinct peak at 20° and nulls at -60° and 85° . A 7-dB difference in amplitude existed between the highest peak and the clearest null at 10 and 12.5 kHz.

Rodent Trapping. Six mammal species were trapped. Their densities (animals per ha \pm S.E.M., based on the Peterson estimators for the two grids) were 28 ± 2.9 for the diurnal striped mouse (*Rhabdomys pumilio*), 13.3 ± 2.6 for the multimammate mouse (*Mastomys natalensis*), 2.7 ± 2.5 for the an-

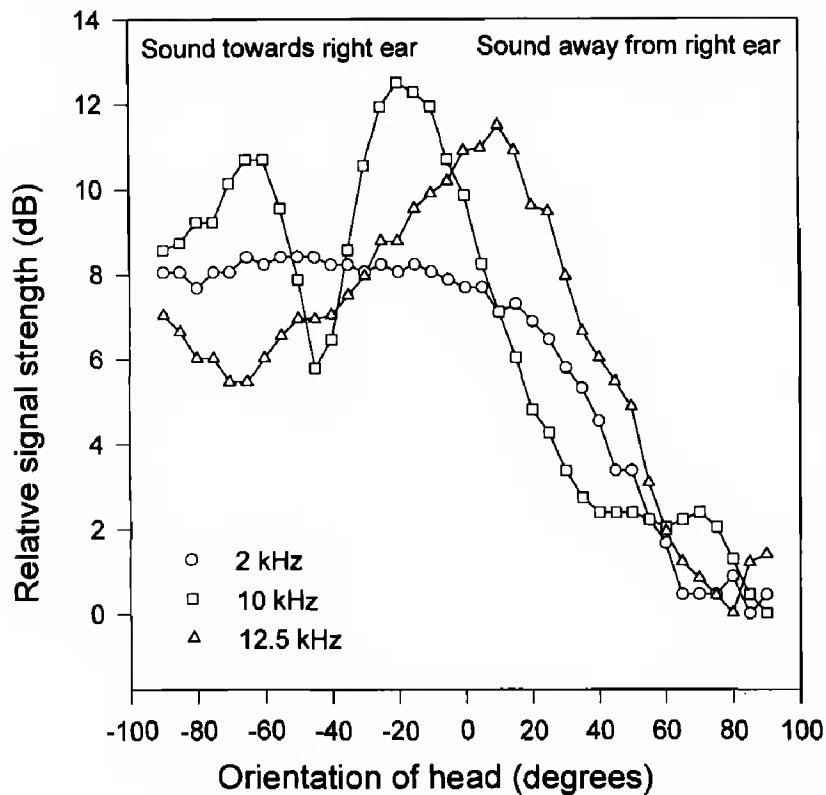


Figure 3. The directional sensitivity of the facial mask of a dead Grass Owl towards pink noise of $\frac{1}{3}$ octave at 2 kHz, 10 kHz and 12.5 kHz. No clear peaks and nulls were evident at 2 kHz, indicating no directional sensitivity at 2 kHz, but which was evident at the higher audio-frequencies.

goni vlei rat (*Otomys angoniensis*), 2.4 ± 2.1 for swamp musk shrew (*Crocidura mariquensis*), 1.3 ± 0.6 for the forest shrew (*Myosorex varius*), and 0.27 ± 0.1 for the grey climbing mouse (*Dendromus melanotis*). The striped mouse was diurnal, the other species nocturnal or crepuscular.

Rodents Subjected to Owl Clicks. For both the 10 sec and entire duration categories, the reactions of the rodents did not differ significantly between the three different treatments (Fig. 4, $\chi^2 < 11.36$; $df = 10$ for each of the nine individuals tested, $P > 0.35$). Most of the rodents either did not move (reaction category one), or they reacted by moving only a short distance (reaction category two). On a few occasions the animals reacted to plover and traffic recordings by running into their burrows (reaction category six, Fig. 4). This reaction was never exhibited in response to the Grass Owl clicks.

DISCUSSION

The repetitive broadband clicks of Grass Owls have a structure which is potentially useful for echolocation. Buchler and Mitz (1980) argued that the signal-to-noise ratio of a signal can be increased by the integration of successive pulses into

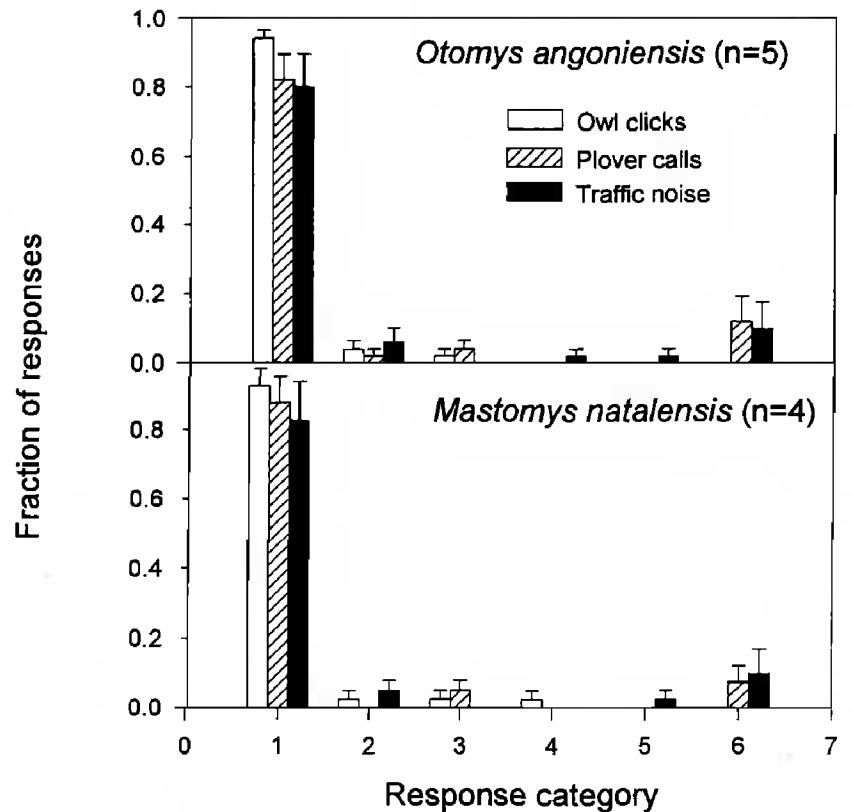


Figure 4. The response of two species of rodents (captured at Rietvlei Dam) towards recordings of Grass Owl clicks and to two other control sounds. Responses during a period of 85 sec following the initiation of a playback are summarized here (see methods). There are no differences in the responses towards the three types of sounds heard by the rodents. Top: *Otomys angoniensis*, Bottom: *Mastomys natalensis*. Bars indicate standard errors of means.

double clicks, allowing for the derivation of relative velocity information. Alternatively, Suthers and Hector (1985) provided a physiological explanation for the use of paired pulses by vocal tract vocalization. Double clicking may also allow individuals to discriminate their echolocation calls from those of others during crowded flights (Fullard et al. 1993); however, Grass Owls defend territories and occur in low numbers. Even though the emphasized frequency of the Grass Owl clicks (1.9 kHz) is lower than that of swiftlets (3–8 kHz; Fenton 1975, Coles et al. 1987, Fullard et al. 1993) and megachiropteran fruit bats (10–17 kHz; Schnitzler and Henson 1980), the temporal characteristics of Grass Owl calls fall within the ranges of other clicking birds. The interval between clicks within double clicks (20 ms) is similar to that of the swiftlets (18 ms; Coles et al. 1987) and megachiropteran fruit bats (18–20 ms; Schnitzler and Henson 1980). The single click duration (12 ms) is much longer than those of swifts (1–3 ms; Fullard et al. 1993), but shorter than the single pulse bursts of Oilbirds (15–20 ms; Konishi and Knudsen 1979). The click

rate for double clicks (7 s^{-1}) appeared to fall within the range used by Cave Swifts ($6\text{--}25 \text{ s}^{-1}$; Medway 1959, Coles et al. 1987), while the click rate for a Grass Owl click train (32 s^{-1}) exceeded this range.

Even though there was structural similarity between Grass Owl clicks and those of other echolocating bird species and bats, several arguments indicated that Grass Owls do not echolocate. First, Grass Owls click while sitting at ground level on their roosts and it is unlikely that such clicks could have an echolocative function. Second, swiftlets and Oilbirds increase their click rates when landing on the nest or when approaching obstacles (Fullard et al. 1993) and when approaching obstacles (Fenton 1975, Konishi and Knudsen 1979). This also occurs in microchiropteran bats (feeding buzz, Jones and Rayner 1990, Miller and Treat 1993) which allows increased resolution of location as the animal approaches the object. No similar increase in click rate has been observed for Grass Owls. In fact, the click rate had a high degree of constancy (Table 1). The owls frequently landed without clicking at all. This contrasts with Erasmus' (1992) finding that the steady pulse rate of flying Grass Owls sometimes increased rapidly when bringing prey to the nest and which probably was related to the presence of chicks, not observed during the present study. Third, there was no correlation between the amount of ambient nocturnal light and the incidence of Grass Owl clicking (Fig. 2). This indicated that clicking is not used to complement visual acuity. In fact, there was a slight trend for increased use of clicking when enough light was available for vision. Fourth, assuming that sound travels at the speed of 350 ms^{-1} in Grass Owl habitat, echos could only travel 4.2 m in 12 ms, the duration of clicks. This would render flying Grass Owls deaf to obstacles within 2.1 m. Assuming that the neural system of the owl can respond within 20 ms, as do some response systems in bats (Suga 1988), Grass Owls should be oblivious of objects closer than about 5 m. This ruled out the echolocation of small, close by objects. Apart from this, open grassland presents few large obstacles which need to be negotiated while hunting. Fifth, the facial mask of the Grass Owl measured in the laboratory was directionally insensitive at 2 kHz (Fig. 3); therefore, it was insensitive to Grass Owl clicks. This can be understood by considering the wavelengths of the frequencies used: 17.2 cm at 2 kHz, 3.4 cm at 10 kHz, and 2.7 cm at 12.5 kHz. It follows that the mask, which has a width of approximately

7 cm, is more directionally sensitive to higher frequencies and implies that echolocation for Grass Owls is not possible at such low audio-frequencies. Although this argument ignores the auditory neural structures and the structure of the internal ear, Payne (1971) showed that Barn Owl auditory acuity during hunting can be explained by the characteristics of the facial mask alone. We conclude that Grass Owls do not use clicking as a means of echolocation.

The fact that Grass Owls were observed flying low and clicking, then stopped clicking, landed, and shortly afterwards resumed the clicking flight could be seen as being supportive of the hypothesis that the clicks aid in hunting. However, it was not certain whether these birds were indeed hunting. Trapping was performed to aid in the choice of rodent prey species used in the experiments. We believe that the use of multimammate mice and vlei rats as experimental subjects is justified by the fact that they were the most abundant nocturnal rodents in the study area and since vlei rats are known preferred prey items of Grass Owls (Kemp and Calburn 1987, Steyn 1982). In other areas, Barn Owls prey on nocturnal species (voles) in relation to their abundance (Campbell et al. 1987).

There was no significant difference in reaction between the three different sound treatments for any of the nine experimental rodents. In fact, the animals in general reacted to none of the sounds (Fig. 4). On a few occasions, they ran into burrows in response to traffic and plover sounds, but not after hearing owl clicks (Fig. 4). The rodents probably reacted to plover and traffic recordings in this way because the latter sounds had a larger dynamic range (becoming louder, then softer) than did the Grass Owl recordings which had more constant characteristics. One might argue that the rodents did not react to recorded clicking calls, but may have reacted to the clicking calls of live Grass Owls. Indeed, Abramsky et al. (1996) found that the strongest response of gerbils (reduction of activity) was to visual stimuli of flying Barn Owls, with weaker responses to recorded hunger calls. However, they were still able to recognize a clear response to recorded owl calls. However, the clicking call of Grass Owls did not stimulate the rodents into activity and it was therefore unlikely to be important in prey capture.

Lack of behavioral reaction by rodents may actually be a response to owl clicks. Even though no evidence of freezing was observed when the ro-

dents heard any of the sound stimuli, this facet of the rodent behavior needs more study within the Grass Owl context. Even though freezing may be adaptive, it does not affect our hypothesis test about prey stimulation.

Our data suggested that Grass Owl clicks have a communicative function toward other Grass Owls. First, we heard owls that double clicked, apparently in response to clicking by another owl, on five occasions. Erasmus (1992) stated that a Grass Owl pair appeared to use their clicking calls to maintain contact with each other while hunting. Second, we observed Grass Owls which emitted click trains while chasing each other on two occasions. Kemp and Calburn (1987) also mentioned bursts of clicking by pairs of flying Grass Owls at the onset of the breeding season, while Erasmus (1992) observed click trains when owls brought prey to their young in the nest. In our study, however, a single bird inhabiting roost 1 was frequently heard clicking while flying within its territory. We speculated that this clicking was a means of making the signaler's presence known to other owls nearby, similar to the behavior of some microchiropteran bats (Leonard and Fenton 1984). Third, the statistically significant differences in clicks of owls at roosts 1 and 2 indicated that significant individual variation existed in call characteristics. While acknowledging that the data for roost 2 are confounded between the two owls roosting there, all the parameters measured at that roost were unimodal and the Mann-Whitney test indicated significant differences in call structure from the two roosts and, by implication, between individual owls. Such individual variation might be audible to Grass Owls, enabling individual recognition by owls. This is consistent with the fact that with microchiropteran bats, echolocation calls are significantly less variable than social calls (Fenton 1994).

Obrist (1995) argued that echolocation has probably evolved from acoustic communication, still serves such functions and could be as flexible. Echolocation signals and some vocalizations following them have a communication function in swifts (Fullard et al. 1993) and Oilbirds (Suthers and Hector 1982, 1985). Fenton (1994) also believed that signals as reliable as those used in echolocation sometimes have a communicative function. Some microchiropteran bats use these signals to eavesdrop in locating vulnerable prey (Balcombe and Fenton 1988), to monitor conspecific intrusions into an area (Leonard and Fenton 1984) and

as a long-range signal advertising its presence in a foraging area (Leonard and Fenton 1984). We believe that, in the case of Grass Owls, clicking is a preadaptation that might potentially constitute raw material from which echolocation in these owls could evolve. However, if the hypothesis of the conspecific communicative function of Grass Owl clicks is robust, the transition from communicative clicks to echolocative sounds has not occurred in the Grass Owl.

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Appendix 1. Parameters used for the analysis of spectral and temporal characteristics of Grass Owl vocalizations.

PROPERTY	MEASUREMENT	
	SPECTRAL	TEMPORAL
Filter bandwidth (Hz)	170.97	638.89
Frame length (ms)	23.22	5.805
Time (ms)	5.805	2.902
Overlap (%)	75	50
Frequency (Hz)	21.53	21.53
FFT size (points)	1024	1024
Windowing function	Hamming	Hamming
Clipping level (dB)	-115	-115